

Host specificity in phylogenetic and geographic space

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The measurement of host specificity goes well beyond counting how many host species can successfully be used by a parasite. In particular, specificity can be assessed with respect to how closely related the host species are, or whether a parasite exploits the same or different hosts across its entire geographic range. Recent developments in the measurement of biodiversity offer a new set of analytical tools that can be used to quantify the many aspects of host specificity. We describe here the multifaceted nature of host specificity, summarize the indices available to measure its different facets one at a time or in combination, and discuss their implications for parasite evolution and disease epidemiology.

Host specificity meets biodiversity

Host specificity, in other words the extent to which parasites can exploit different host species, is one of the most fundamental properties of parasitic organisms. For instance, it is a key determinant of how likely parasites are to persist following host extinction [1,2], or to become established following their introduction into new areas [3,4]. Recent genetic and experimental investigations have revealed that for many parasite species, host specificity is often either under- or overestimated when based on field surveys alone [5]. Even when accurate, however, the traditional measurement of host specificity as the mere number of host species that can be used by a parasite greatly limits our ability to understand its evolution and its ecological implications. For instance, can one truly appreciate how specialized a parasite is without considering the relationships between its few host species, or without addressing why it uses different hosts in different geographic areas? Similar questions have been raised regarding the measurement of biodiversity, for which mere species counts are now often seen to be insufficient [6]. Indeed, the concept of biodiversity encompasses many facets, including phylogenetic and functional differences between species and their turnover across space [7]. In this review we develop a hierarchical and multifaceted view of host specificity that parallels the rigorous approach now

used for the measurement of biodiversity. First, we dissect host specificity into its various components, each manifested at different scales, to highlight the many nuances of specificity. Second, the indices and analytical approaches that recently became available to measure various facets of host specificity and investigate their associations are summarized. Finally, the evolutionary pressures shaping different aspects of host specificity and their ecological implications are discussed.

The many facets of host specificity

Two parasite species exploiting the same number of host species could appear to have identical host specificity, whereas in fact their plasticity in host use can differ at numerous levels. Similarities among different parasites in the number of host species exploited, or basic host specificity in its traditional sense and as used in many earlier studies, can mask fundamental differences either in the relative ecological importance of each host for the parasite population, in their phylogenetic closeness to each other, or in variation in host use on geographical scales. In the discussion of these various facets of host specificity that follows, we employ the term 'host' to refer only to those species in which a parasite can successfully survive, grow and/or reproduce; we ignore 'accidental' hosts in which parasites cannot develop, because these do not really belong to the repertoire of the parasite.

Structural specificity

Consider two related parasite species, A and B, each using the same number of host species – for example, four host species. However, their populations are structured differently across their host species; parasite A achieves roughly similar prevalence and abundance in all four of its hosts, whereas B is highly abundant in one host species but rare in the other three. Therefore, parasite B displays higher structural specificity than A because the bulk of its population utilizes a single host species (Figure 1). The uneven distribution of a parasite population between two or more host species is commonly observed in both terrestrial and aquatic ecosystems. For example, the mean abundance of several species of helminths and copepods differs substantially, often by a factor of 10-fold or more, between different

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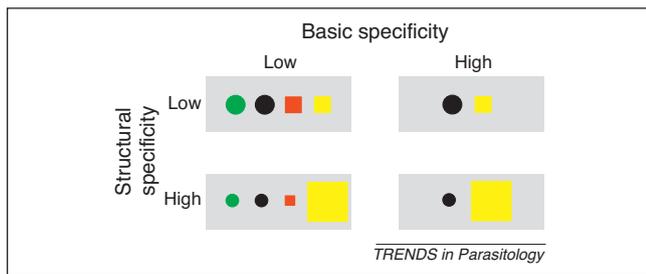


Figure 1. Contribution of the population structure of a parasite to the measurement of host specificity. Here, a parasite population consists of all conspecific parasites at the same life cycle stage occurring in all suitable sympatric hosts in a distinct geographical area. Different parasite populations (shaded boxes) can exploit few or many host species (colored symbols), which represents their basic host specificity in the traditional sense. However, the parasite populations can also be characterized by their structural specificity: they have low structural specificity if all host species harbor similar proportions of the total parasite population (proportional to the size of the symbols), and high structural specificity if most parasite individuals are concentrated in one or very few host species.

sympatric flatfish species inhabiting coastal Portuguese waters [8]. Similarly, the mean abundance of the ectoparasitic mite, *Spinturnix myoti*, is about 35% higher on one of its two sibling bat host species, although the prevalence of infection is identical in both hosts [9]. Indices of host specificity have been developed specifically to account for these differences [10], although the widely used indices of species diversity that incorporate both the number of species and the evenness of their abundances, such as the Simpson or Shannon indices [6], would be excellent indices of structural host specificity when applied to data on relative host use.

Phylogenetic specificity

Consider now another two related parasite species, A and B, each using four host species and achieving roughly equal abundance in all their hosts. However, the hosts of parasite A belong to distantly related families, whereas those of parasite B all belong to the same genus. Therefore, we can easily argue that parasite B displays higher phylogenetic specificity than A because its hosts are restricted to a narrower phylogenetic spectrum (Figure 2). There are numerous examples of parasites that are either restricted to a few closely related host species, or are capable of exploiting completely unrelated host taxa. For example, the nematode *Trichostrongylus axei* occurs predominantly in ungulates but can also infect mammals from other orders [11], whereas acanthocephalans parasitic in fishes can typically exploit hosts from completely different families [12]. Existing indices of phylogenetic biodiversity [13–16] could easily be applied in such situations to distinguish between parasites with different levels of specificity, and indeed they have been used for that purpose [17]. Alternatively, an index of phylogenetic host specificity has also been proposed [18]. Whether designed for measuring biodiversity or host specificity, essentially all these indices compute either the average or total phylogenetic (or taxonomic in the absence of explicit branch length data) distance between all possible pairs of host species used by a parasite, to estimate their phylogenetic distinctness.

As an extra step, it is relatively easy to combine data on phylogenetic relatedness and data on relative abundances,

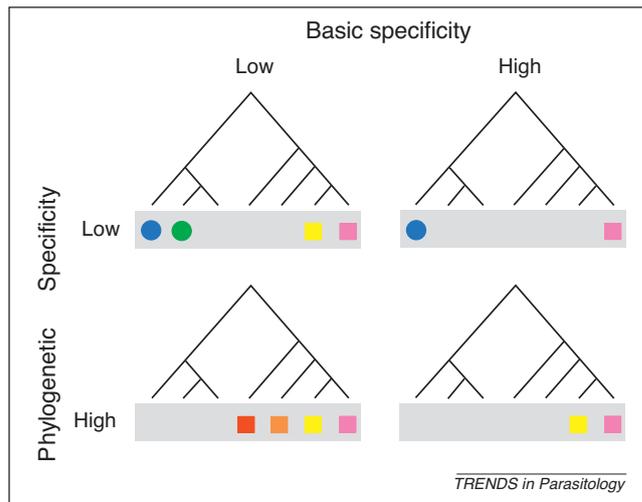


Figure 2. Contribution of host phylogeny to the measurement of host specificity. For any given number of host species (colored symbols) used by a parasite population (shaded boxes), in other words for any level of basic host specificity, a parasite could show high phylogenetic specificity if it only exploits host species closely related to each other, or low phylogenetic specificity if its host species are not closely related. In these examples, structural specificity, based on the distribution of parasite individuals among host species, is assumed to be the same in all cases.

that is, to combine structural specificity and phylogenetic specificity into a single index of structural phylogenetic specificity. Again, this can be achieved either by applying methods designed for the study of biodiversity [19–21] or by using the related indices developed specifically for the measurement of host specificity [17,22]. Here again the average or total phylogenetic distance is calculated among all host species, but proportionally greater weight is given to host species in which the parasite achieves greater abundance. Thus, if a parasite achieves high abundance in two congeneric hosts but low abundance in two other hosts from another family, its combined phylo-structural specificity will be higher than if, all else being equal, it had reached high abundance in one host from each family.

Specificity in geographic space

Finally, it is worth considering host specificity on a geographic scale. Across its geographic range, any parasite species will be exposed to communities of potential host species that change in composition and relative density from one locality to the next [23]. Specificity can thus also be manifested as the consistency in host use across a changing host landscape. For example, imagine that in one area parasite species A and B each use four host species, of similar phylogenetic relatedness, and achieve roughly equal abundance in all their hosts. However, in a different locality, parasite B uses the same four host species whereas A uses four completely different host species. Therefore, although both parasites have similar structural and phylogenetic host specificity, parasite B displays higher host specificity than A across its geographical range, because its use of hosts from the available species pool is clearly more limited both locally and globally. Again, this hypothetical scenario is often seen in nature. For example, consider the two fleas *Mesopsylla hebes* and *Oropsylla ilovaiskii* which, on average, both

exploit only two host species in each locality where they occur. However, across their geographic ranges, the vast majority of hosts harboring the former flea species belong to a single rodent family, Dipodidae, whereas the latter flea is found on rodents belonging to three different families [24].

Research on biodiversity recognizes this spatial dimension. Ecologists now distinguish between local species diversity, or α -diversity, and the difference in species composition among localities, or β -diversity, which captures the turnover of species in geographical space [6,25–27]. Similarly, we can distinguish between α -specificity, or the host specificity shown by a parasite in one locality, and β -specificity, or the spatial turnover in host species used across localities [24]. Thus, particular parasite species can show high specificity at a local scale while being generalists on a global scale, or vice versa. In addition, once again in parallel to the measurement of biodiversity in space, one can compute an overall measure of host specificity, or γ -specificity, across the entire geographical range of a parasite, based on the total list of host species used across all localities where the parasite occurs.

Just as with biodiversity measures [28,29], the basic, structural and phylogenetic components of host specificity can be combined into multidimensional measures, and treated at α , β and/or γ geographical scales (Figure 3). Depending on the completeness of the data available, host specificity can be investigated in one or more dimensions at a time. For example, data on the occurrence of parasite species in various host species could be limited to presences and absences, but they could also include actual abundances. If abundance data are available for numerous localities, it is the relative abundance of a parasite in its different sympatric hosts, and not the absolute abundance, that matters in geographical comparisons – because absolute

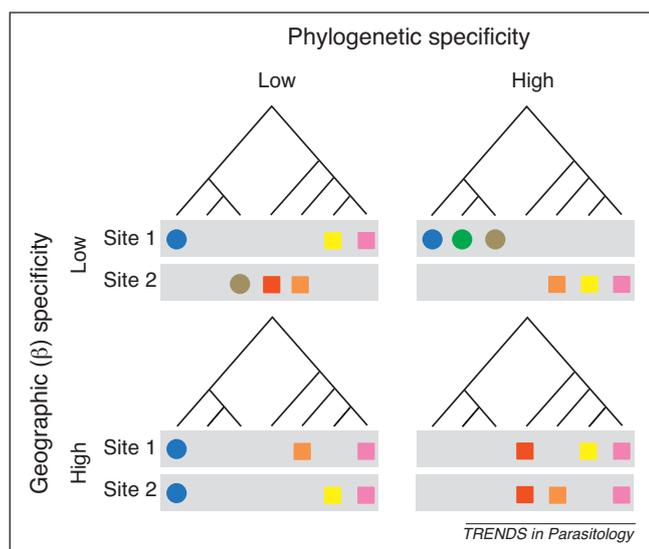


Figure 3. Host specificity in geographic space. For each of four parasite species, host use in two separate populations (adjacent shaded boxes) from distinct geographical sites is shown. For any level of phylogenetic specificity, which depends on host relatedness, a parasite can show low geographic specificity (i.e. β -specificity) if the identity of the host species (colored symbols) it uses varies among localities, or high β -specificity if it exploits the same host species everywhere. In these examples, both basic and structural specificity, based on the number of host species used and the distribution of parasite individuals among host species, respectively, are assumed to be the same in all cases.

abundance could vary due to the effects of environmental conditions on infective stages. Indices and measures of host specificity are available for all levels of complexity, whether focused on a single component of specificity or on all of them, and at any spatial scale (Box 1). There are also programs available for the computation of all these measures (Box 2).

There are other facets of host specificity, of course, beyond those discussed above. For instance, in helminths with complex life cycles, different sets of host species are used at different stages of the life cycle, adding an ontogenetic component to host specificity. However, because most interspecific analyses seeking to understand the ecology and evolution of host specificity compare the specificity of different parasite species at a given developmental stage, this ontogenetic component will not be discussed further.

Evolutionary and ecological implications of host specificity

Deconstructing host specificity into its structural, phylogenetic and spatial components opens up several new research possibilities [30]. It will not only allow us to generate more precise and targeted hypotheses about host–parasite ecology and evolution, but also provide the tool-kit to test them. In particular, the measurement of separate facets of host specificity will increase the value of comparative analyses, which have long been powerful approaches in evolutionary biology [31]. These are founded on relationships between variables measured in different localities or across species, to evaluate the contribution of various factors to intra- or interspecific variation, respectively. It will now be possible to precisely match a putative selective factor with the specific facet of host specificity on which it is presumed to act.

The first step, however, will be to determine how different aspects of host specificity are correlated with each other across different parasite species. The subset of species used as hosts within a local host community is not a random subset of those available: typically, parasites infect host species more closely related to each other than if host selection was completely random [32]. However, as more host species are added to the repertoire of a parasite the breadth of their phylogenetic spectrum invariably increases, leading to weak but significant interspecific correlations between basic and phylogenetic measures of host specificity [18,33]. Also, two closely related host species are more likely to harbor similar abundances of a given parasite species than two unrelated hosts, and this is true whether the parasites are helminths [34] or arthropods [35]. Therefore, we might expect a negative relationship between measures of structural and phylogenetic host specificity (Figure 4), if a parasite population is apportioned more unevenly among host species when the latter belong to different genera or families. Similarly, there are correlations between the different measures of biodiversity used in ecology and conservation [7,36]. It will be essential to assess the statistical independence of different facets of host specificity using comparative analyses before their full potential can be realized.

It is important to determine which selective forces shape the different facets of host specificity, and which are most

Box 1. Host specificity indices in phylogenetic and geographic space

Host specificity is inversely proportional to ‘generalism’ in host use, and it is the extent to which parasites are generalists that is measured by most indices. Hence, for the indices we recommend below, low index values correspond to high host specificity, and vice versa.

1. Basic and structural host specificity

Traditionally, host specificity is simply estimated as the number of host species (*S*) used by a parasite species, but this value can also be corrected for biases arising from the undersampling of rare hosts using the Chao indices [62]. When data on prevalence or abundance can be incorporated into the measurement of structural specificity, we suggest using composite indices such as the Shannon index, or else a ‘pure’ evenness index, independent from the number of host species, such as the Bulla index [63].

2. Phylogenetic host specificity, or phylosppecificity

Because host species are phylogenetically related, we can estimate the phylogenetic host specificity of a parasite, *PS_i*, as the phylogenetic diversity of its hosts, which is equivalent to the measure *PD_i* of the biodiversity literature. Here, *PS_i* represents the total length of branches linking the host species of parasite *i* along the phylogenetic tree [13,64].

Because *PS_i* is not totally independent from the number of host species used by a parasite and thus provides information redundant with *S*, two options are possible.

(i) Estimate the standardized effect size of *PS_i*, or *SPS_i*, using random subsets of potential host species drawn from the regional pool to determine whether the hosts actually used by the parasite are more or less closely related than expected by chance, and thus whether the phylosppecificity of parasite *i* is high or low for a given value of *S* using:

$$SPS_i = \frac{(PS_i - \overline{PS_{sim}})}{SD(PS_{sim})} \tag{1}$$

where *PS_i* is the observed phylosppecificity of parasite *i*, $\overline{PS_{sim}}$ is the mean phylosppecificity of all random host subsets, and *SD(PS_{sim})* is the standard deviation of all randomized phylosppecificity values.

(ii) Estimate phylosppecificity as the average phylogenetic distinctiveness, *SPD_i*, between all pairs of host species [18], which is independent from how many host species are used by a parasite:

$$SPD_i = 2 \frac{\sum_{j < k} \omega_{jk}}{S(S-1)} \tag{2}$$

where ω_{jk} is the phylogenetic distance between host species *j* and *k* used by parasite *i*, or, when the phylogeny is not fully resolved, the number of taxonomic steps required to reach a node common to both.

The double summation is over the set $\{k = 1, \dots, S; j = 1, \dots, S, \text{ such that } j < k\}$ in order to consider all host species pairs.

3. Geographic host specificity, or β-specificity

Measuring the turnover of host species used by a parasite among different localities, in other words β-specificity or *BS_i*, involves estimating the dissimilarity in host species identities between localities. Most dissimilarity or β-specificity indices have been designed for two samples only [65]. Ideally, estimates of β-specificity across space should include several samples (i.e. data from different localities [24]). We suggest using the extension of the Sørensen dissimilarity index for multiple-sites [66] to measure β-specificity:

$$BS_i = 1 - \frac{T}{T-1} \left(1 - \frac{S_T}{\sum_t S_t} \right) \tag{3}$$

where *T* is the number of samples or localities, *S_t* is the number of host species used in locality *t*, and *S_T* the total number of host species used by parasite species *i* across all *T* localities (i.e. the regional host pool). If parasite *i* exploits the same host species across all localities, then *S_t* = *S_T* and *BS_i* = 0. If parasite *i* uses totally different host species from one locality to the next, then $S_T = \sum_t S_t$ and *BS_i* = 1.

4. Combining phylogenetic and geographic specificity: phylobetasppecificity

Information about the phylogenetic relatedness of host species and their different use across localities can be combined into a single index of phylogenetic β-specificity, or *PBS_i*. This corresponds to the phylogenetic turnover of host species used by parasite *i* over geographic space. For this, we can use an extension of the Sørensen index [66] to branches instead of species following the principle underlying the construction of the Phylsor index [67]:

$$PBS_i = 1 - \frac{T}{T-1} \left(1 - \frac{PD_T}{\sum_t PD_t} \right) \tag{4}$$

where *T* is the number of samples or localities, *PD_i* is the phylogenetic diversity of host species used by the parasite in locality *t*, and *PD_T* the phylogenetic diversity of all host species used by parasite species *i* across all *T* localities. If parasite *i* exploits the same host species over all localities, we obtain *PD_t* = *PD_T* and *PBS_i* = 0. If parasite *i* uses different host species from one locality to the next, then the less phylogenetically related those hosts are, the higher the *PBS_i* value.

We opted to present a common statistical framework using the Sørensen index because it can cope with multiple localities [66] and can incorporate phylogenetic diversity [67]. If prevalences are known for each host species used by a parasite, an alternative framework could be developed to estimate specificity over geographic and phylogenetic space while also incorporating structural host specificity (see main text), based for instance on the Rao index [7,68,69] or the Shannon entropy index [60]; however, this is beyond the scope of the present summary.

important at each spatial scale. For instance, we might expect that unstable host communities, characterized by population densities that fluctuate substantially over time because of seasonal migration or reproduction, should favor parasites with low phylogenetic specificity but no particular pattern of structural specificity, because parasite populations would need to use hosts in proportion to their current densities in order to persist. Current work on such unstable host–parasite systems [37] has yet to consider host specificity beyond the simple number of host species used, and thus such predictions remain untested. In addition, we might expect that selected host or parasite properties, in particular dispersal abilities, could drive patterns of geographical specificity. Host mobility has already been shown to homogenize parasite community

composition across spatially distant localities [38,39], but its impact upon various facets of host specificity, especially α- and β-specificity, remains unknown.

Conversely, we can ask what phenomena are likely to result from certain combinations of structural, phylogenetic and geographic host specificity. Both the evolution of parasite virulence [40,41] and the strength of local adaptation [42,43] are known from theoretical and empirical work to relate to host specificity. However, previous studies have considered host specificity in its most basic sense, in other words the number of host species used, and the importance of different components of host specificity for these evolutionary processes is likely to vary. One can imagine that local adaptation of parasites to their hosts, whatever the number of host species, would be facilitated

Box 2. Practical tools to measure host specificity

We suggest to use two R packages to compute all indices presented in Box 1. First, the package 'vegan' allows one to estimate:

1. Basic host specificity, i.e. the number of host species used by a parasite in a locality, with the function *specnumber*. The function *estimateR* then allows a correction for biases arising from the undersampling of rare species that could escape detection as hosts.
2. Structural host specificity, with a composite index such as Shannon or Simpson using the function *diversity*.
3. Phylogenetic distinctiveness among host species, or SPD_i , with the function *taxondive* which requires the taxonomic (or the phylogenetic) distances between all host species pairs as an input file.

Second, the package 'picante' allows one to estimate:

1. The phylogenetic diversity of the host species exploited by parasite i (PD_i) using the function *pd*. The phylogenetic tree required as input needs to be ultrametric.
2. The standardized effect size of the phylogenetic diversity of hosts exploited by parasite i (SPS_i) using the function *ses.pd* and shuffling taxa labels in the host phylogenetic tree. The phylogenetic tree also needs to be ultrametric.
3. The Rao index, through the function *raoD*, which allows inclusion of prevalence data to compute specificity indices over space and phylogeny.

by high phylogenetic specificity, and/or by high structural specificity, because these would involve a single host species driving parasite population dynamics. Along those lines, some components of host specificity appear to be more relevant than others to the assumed trade-off between how many hosts a parasite exploits and its performance in any of them or its average performance across all of them, captured by the phrase 'jack of all trades but master of none' [44]. Indeed, although physiological incompatibilities between host and parasite can greatly affect this trade-off [45], at the macroecological scale if the trade-off exists, it can be more easily revealed using a measure of phylogenetic specificity than the simpler basic measure [46]. Thus, the newly available measures of all facets of

host specificity now allow more sophisticated tests of old evolutionary hypotheses.

Several epidemiological processes are also closely linked with one or more facets of host specificity. However, which components of host specificity are the most important for parasite population dynamics, and which are more important as a hedge against extinction? Structural specificity, in other words data on relative abundance in different host species, is used to estimate the probable number of host plants exploited by phytophagous insects and identify those species most at risk of extinction [47]; the same analysis could be carried out for animal parasites. In the context of managing diseases, which components of host specificity are most relevant for the risk of parasite establishment and emerging infectious disease following biological invasions or climate change? Parasites can re-adjust their host range after changes in geographical distribution or local ecology, so as to align themselves with the new set of suitable hosts they encounter [48]. This process of ecological fitting provides a framework for host-switching and the establishment of new host-parasite associations in the face of environmental change [49,50]. However, the deconstruction of host specificity into quantifiable facets gives it more predictive power. It would be possible, for example, to measure precisely the current phylogenetic specificity of a parasite to determine the likelihood that it would spread to other hosts if introduced to a new area, by measuring the phylogenetic distances between potential hosts and the current host suite. Similarly, measuring structural specificity before local changes in relative host abundances would allow more robust predictions of the likelihood of local parasite persistence.

Concluding remarks

As discussed above, taking a multifaceted look at host specificity creates exciting new opportunities for ecological and evolutionary parasitology. At a time when host specificity is recognized as a key factor determining the spread of parasitic diseases in the face of biological invasions, loss of natural habitats and climate change [51], its dissection into distinct and measurable facets paves the way toward a better understanding of the processes that control which hosts a parasite can use. Experimental studies of model species will always remain important to determine, at a proximate level, how given environmental features affect host use by generalist parasites [52,53]. The analytical tools presented here will empower large-scale studies addressing the causes of variation in host specificity among parasite species. At the moment, however, interspecific patterns revealing how different aspects of host specificity covary with environmental factors or other parasite properties have only been investigated for very few parasite taxa, predominantly avian malaria [17,54] and fleas parasitic for mammals [44,55,56]. Large comparative datasets on other parasite groups are urgently needed to explore the several levels on which pathogens can either specialize or turn into generalists.

Another important future direction will be the further expansion of our outlook on host specificity. In recent years, ecologists and conservation biologists have started to consider biodiversity not only from a numerical or phyloge-

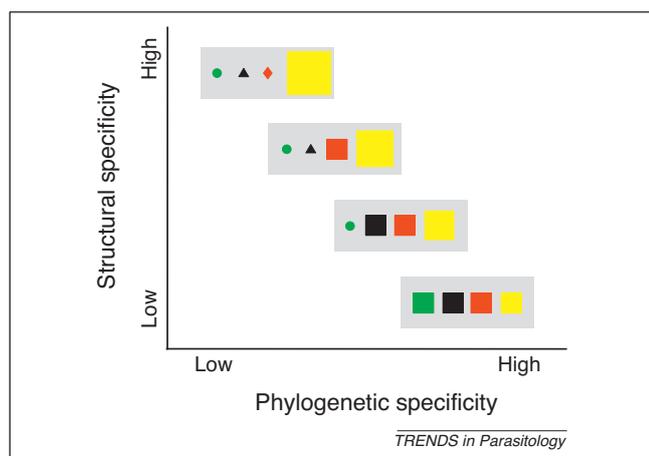


Figure 4. Hypothesized relationship between structural and phylogenetic components of host specificity. If different parasites (shaded boxes) use the same number of host species (colored symbols), but some use hosts belonging to different higher taxa (genera or families, indicated by different symbol shapes) whereas others use hosts from the same taxon, a negative relationship is expected between structural specificity and phylogenetic specificity. This is expected if the abundance (proportional to the size of the symbols) achieved by parasites in their hosts is constrained by physiological and other factors.

netic perspective, but also from a functional one [57,58]. Several indices have been developed to measure the functional diversity of species assemblages, that is, the diversity of ecological or phenotypic traits that characterize them [59,60]. To borrow once more from biodiversity research, we could envisage the measurement of functional host specificity, by quantifying the similarities among the hosts of a parasite in terms of the functional traits they share rather than their phylogenetic relationships. Furthermore, most indices that can be used to measure phylogenetic specificity can be adapted to measure functional specificity [29] because they are based on distances between species pairs and trees built from traits [61]. For studies of generalist parasites in taxon-rich host communities, this might allow more explicit links between host ecology and host-switching by parasites. The take-home message here is that specialization by parasites can occur at several levels, and that whatever the question we pose, we must make sure to use the proper analytical tools to answer it.

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References

- Dunn, R.R. *et al.* (2009) The sixth mass coextinction: are most endangered species parasites and mutualists? *Proc. R. Soc. Lond. B: Biol. Sci.* 276, 3037–3045
- Moir, M.L. *et al.* (2010) Current constraints and future directions in estimating coextinction. *Conserv. Biol.* 24, 682–690
- Taraschewski, H. (2006) Hosts and parasites as aliens. *J. Helminthol.* 80, 99–128
- Dunn, A.M. (2009) Parasites and biological invasions. *Adv. Parasitol.* 68, 161–184
- Poulin, R. and Keeney, D.B. (2008) Host specificity under molecular and experimental scrutiny. *Trends Parasitol.* 24, 24–28
- Magurran, A.E. and McGill, B.J. (2011) *Biological Diversity: Frontiers in Measurement and Assessment*, Oxford University Press
- Devictor, V. *et al.* (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.* 13, 1030–1040
- Marques, J.F. *et al.* (2011) Host–parasite relationships in flatfish (Pleuronectiformes) – the relative importance of host biology, ecology and phylogeny. *Parasitology* 138, 107–121
- Christe, P. *et al.* (2003) Differential species-specific ectoparasitic mite intensities in two intimately coexisting sibling bat species: resource-mediated host attractiveness or parasite specialization? *J. Anim. Ecol.* 72, 866–872
- Rohde, K. and Rohde, P.P. (2008) How to measure ecological host specificity. *Vie Milieu* 58, 121–124
- Archie, E.A. and Ezenwa, V.O. (2011) Population genetic structure and history of a generalist parasite infecting multiple sympatric host species. *Int. J. Parasitol.* 41, 89–98
- Kvach, Y. and Sasal, P. (2010) *Telosentis exiguus* (von Linstow, 1901) (Palaecanthocephala: Illiosentidae), a generalist parasite of fishes in the Mediterranean basin. *Syst. Parasitol.* 76, 9–18
- Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10
- Clarke, K.R. and Warwick, R.M. (2001) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Mar. Ecol. Prog. Ser.* 216, 265–278
- Helmus, M. *et al.* (2007) Phylogenetic measures of biodiversity. *Am. Nat.* 169, E68–E83
- Cadotte, M.W. *et al.* (2010) Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. *Ecol. Lett.* 13, 96–105
- Fallon, S.M. *et al.* (2005) Host specialization and geographic localization of avian malaria parasites: a regional analysis in the Lesser Antilles. *Am. Nat.* 165, 466–480
- Poulin, R. and Mouillot, D. (2003) Parasite specialization from a phylogenetic perspective: a new index of host specificity. *Parasitology* 126, 473–480
- Weikard, H. *et al.* (2006) Diversity measurement combining relative abundances and taxonomic distinctiveness of species. *Divers. Distrib.* 12, 215–217
- Allen, B. *et al.* (2009) A new phylogenetic diversity measure generalizing the Shannon index and its application to phyllostomid bats. *Am. Nat.* 174, 236–243
- Cadotte, M.W. and Davies, J.T. (2010) Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Divers. Distrib.* 16, 376–385
- Poulin, R. and Mouillot, D. (2005) Combining phylogenetic and ecological information into a new index of host specificity. *J. Parasitol.* 91, 511–514
- Krasnov, B.R. *et al.* (2011) Scale-dependence of phylogenetic signal in ecological traits of ectoparasites. *Ecography* 34, 114–122
- Krasnov, B.R. *et al.* (2011) Beta-specificity: the turnover of host species in space and another way to measure host specificity. *Int. J. Parasitol.* 41, 33–41
- Jost, L. (2007) Partitioning diversity into independent α and β components. *Ecology* 88, 2427–2439
- McKnight, M.W. *et al.* (2007) Putting beta-diversity on the map: broad-scale congruence and coincidence in the extremes. *PLoS Biol.* 5, e272
- Baselga, A. (2010) Partitioning the turnover and nestedness components of beta-diversity. *Global Ecol. Biogeogr.* 19, 134–143
- Graham, C.H. and Fine, P.V.A. (2008) Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecol. Lett.* 11, 1265–1277
- Mouchet, M.A. and Mouillot, D. (2011) Decomposing phylogenetic entropy into α , β and γ components. *Biol. Lett.* 7, 205–209
- Krasnov, B.R. *et al.* (2010) Deconstructing spatial patterns in species composition of ectoparasite communities: the relative contribution of host composition, environmental variables and geography. *Global. Ecol. Biogeogr.* 19, 515–526
- Freckleton, R.P. and Pagel, M. (2010) Recent advances in comparative methods. In *Social Behaviour: Genes, Ecology and Evolution* (Székely, T. *et al.*, eds), pp. 110–126, Cambridge University Press
- Krasnov, B.R. *et al.* (2004) Geographical variation in host specificity of fleas (Siphonaptera) parasitic on small mammals: the influence of phylogeny and local environmental conditions. *Ecography* 27, 787–797
- Krasnov, B.R. *et al.* (2006) Resource predictability and host specificity in fleas: the effect of host body mass. *Parasitology* 133, 81–88
- Poulin, R. (2005) Relative infection levels and taxonomic distances among the host species used by a parasite: insights into parasite specialization. *Parasitology* 130, 109–115
- Krasnov, B.R. *et al.* (2004) Relationships between parasite abundance and the taxonomic distance among a parasite's host species: an example with fleas parasitic on small mammals. *Int. J. Parasitol.* 34, 1289–1297
- Purvis, A. and Hector, A. (2000) Getting the measure of biodiversity. *Nature* 405, 212–219
- Morgan, E.R. *et al.* (2007) Parasite transmission in a migratory multiple host system. *Ecol. Model.* 200, 511–520
- Thieltges, D.W. *et al.* (2009) Distance decay of similarity among parasite communities of three marine invertebrate hosts. *Oecologia* 160, 163–173
- Poulin, R. and Krasnov, B.R. (2010) Similarity and variability of parasite assemblages across geographical space. In *The Biogeography of Host–Parasite Interactions* (Morand, S. and Krasnov, B.R., eds), pp. 115–127, Oxford University Press
- Gandon, S. (2004) Evolution of multihost parasites. *Evolution* 58, 455–469
- Barrett, L.G. *et al.* (2009) Continua of specificity and virulence in plant host–pathogen interactions: causes and consequences. *New Phytol.* 183, 513–529

- 42 Gandon, S. (2002) Local adaptation and the geometry of host–parasite coevolution. *Ecol. Lett.* 5, 246–256
- 43 Lajeunesse, M.J. and Forbes, M.R. (2002) Host range and local parasite adaptation. *Proc. R. Soc. Lond. B: Biol. Sci.* 269, 703–710
- 44 Krasnov, B.R. *et al.* (2004) Ectoparasitic ‘jacks-of-all-trades’: relationship between abundance and host specificity in fleas (Siphonaptera) parasitic on small mammals. *Am. Nat.* 164, 506–516
- 45 Cobey, S. *et al.* (2010) Ecological factors driving the long-term evolution of influenza’s host range. *Proc. R. Soc. Lond. B: Biol. Sci.* 277, 2803–2810
- 46 Straub, C.S. *et al.* (2011) Evidence for a trade-off between host-range breadth and host-use efficiency in aphid parasitoids. *Am. Nat.* 177, 389–395
- 47 Vesik, P.A. *et al.* (2010) How many hosts? Modelling host breadth from field samples. *Methods Ecol. Evol.* 1, 292–299
- 48 Hoberg, E.P. and Brooks, D.R. (2008) A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host–parasite systems. *J. Biogeogr.* 35, 1533–1550
- 49 Brooks, D.R. and Ferrao, A.L. (2005) The historical biogeography of coevolution: emerging infectious diseases are evolutionary accidents waiting to happen. *J. Biogeogr.* 32, 1291–1299
- 50 Brooks, D.R. and Hoberg, E.P. (2007) How will global climate change affect parasite-host assemblages? *Trends Parasitol.* 23, 571–574
- 51 Agosta, S.J. *et al.* (2010) How specialists can be generalists: resolving the ‘parasite paradox’ and implications for emerging infectious disease. *Zoologia* 27, 151–162
- 52 Kuris, A.M. *et al.* (2007) An experimental evaluation of host specificity: the role of encounter and compatibility filters for a rhizocephalan parasite of crabs. *Int. J. Parasitol.* 37, 539–545
- 53 Koehler, A.V. *et al.* (2011) Genetic and environmental determinants of host use in the trematode *Maritrema novaezealandensis* (Microphallidae). *Parasitology* 138, 100–106
- 54 Hellgren, O. *et al.* (2009) A jack-of-all-trades and still a master of none: prevalence and host range in avian malaria and related blood parasites. *Ecology* 90, 2840–2849
- 55 Krasnov, B.R. *et al.* (2005) Host specificity and geographic range in haematophagous ectoparasites. *Oikos* 108, 449–456
- 56 Krasnov, B.R. *et al.* (2008) Latitudinal gradients in niche breadth: empirical evidence from haematophagous ectoparasites. *J. Biogeogr.* 35, 592–601
- 57 Flynn, D.F.B. *et al.* (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett.* 12, 22–33
- 58 Mouillot, D. *et al.* (2011) Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE* 6, e17476
- 59 Mason, N.W.H. *et al.* (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111, 112–118
- 60 Mouchet, M.A. *et al.* (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct. Ecol.* 24, 867–876
- 61 Mouchet, M. *et al.* (2008) Towards a consensus for calculating dendrogram-based functional diversity indices. *Oikos* 117, 794–800
- 62 Chao, A. (1987) Estimating the population size for capture–recapture data with unequal catchability. *Biometrics* 43, 783–791
- 63 Smith, B. and Wilson, J.B. (1996) A consumer’s guide to evenness indices. *Oikos* 76, 70–82
- 64 Kembel, S.W. *et al.* (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26, 1463–1464
- 65 Koleff, P. *et al.* (2003) Measuring beta diversity for presence-absence data. *J. Anim. Ecol.* 72, 367–382
- 66 Diserud, O.H. and Odegaard, F. (2007) A multiple-site similarity measure. *Biol. Lett.* 3, 20–22
- 67 Bryant, J.A. *et al.* (2008) Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. *Proc. Natl Acad. Sci. U.S.A.* 105, 11505–11511
- 68 Rao, C.R. (1982) Diversity and dissimilarity coefficients: a unified approach. *Theor. Popul. Biol.* 21, 24–43
- 69 Ricotta, C. and Szeidl, L. (2009) Diversity partitioning of Rao’s quadratic entropy. *Theor. Popul. Biol.* 76, 299–302